Effects of insecticide exposure on movement and population size estimates of predatory ground beetles (Coleoptera: Carabidae)

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Abstract

BACKGROUND: Estimates of arthropod population size may paradoxically increase following insecticide applications. Research with ground beetles (Coleoptera: Carabidae) suggests that such unusual results reflect increased arthropod movement and capture in traps rather than real changes in population size. However, it is unclear whether direct (hyperactivity) or indirect (prey-mediated) mechanisms produce increased movement.

RESULTS: Video tracking of *Scarites quadriceps* Chaudior indicated that brief exposure to lambda-cyhalothrin or tefluthrin increased total distance moved, maximum velocity and percentage of time moving. Repeated measurements on individual beetles indicated that movement decreased 240 min after initial lambda-cyhalothrin exposure, but increased again following a second exposure, suggesting hyperactivity could lead to increased trap captures in the field. Two field experiments in which ground beetles were collected after lambda-cyhalothrin or permethrin application attempted to detect increases in population size estimates as a result of hyperactivity. Field trials used mark–release–recapture methods in small plots and natural carabid populations in larger plots, but found no significant short-term (<6 day) increases in beetle trap captures.

CONCLUSION: The disagreement between laboratory and field results suggests mechanisms other than hyperactivity may better explain unusual changes in population size estimates. When traps are used as a primary sampling tool, unexpected population-level effects should be interpreted carefully or with additional data less influenced by arthropod activity.
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1 INTRODUCTION

The unintended effects of insecticides on invertebrates have long been acknowledged as important considerations in pest management. Pest resurgence and secondary pest outbreaks are among the best-known undesirable consequences of insecticide use,[1] and are often attributed to high mortality of predators and parasitoids. However, arthropod responses to sublethal insecticide exposure are both common and varied.[2–4] For example, estimates of natural enemy population size sometimes paradoxically increase following insecticide applications.[5,6]

If traps are used for sampling, apparent increases in arthropod abundance may reflect a surge in movement, as traps measure a combination of activity and abundance (activity–density).[7] In field studies with ground beetles (Coleoptera: Carabidae), increases in pitfall trap captures following insecticide application appear to be particularly common.[6,8–11] Both indirect and direct mechanisms may link insecticides to changes in beetle movement. Indirect mechanisms include changes to mobility, distribution and abundance of prey. For example, Bel'skaya *et al*.[11] noted an increase in ground beetle captures 17 days after a pyrethroid application and suggested carabids moved into the insecticide-treated plots to feed on dead or impaired insects. Chiverton[9] explained similar results in another way, noting that the insecticidal elimination of prey likely increased carabid hunger, leading to increased activity and capture in pitfall traps. However, a direct stimulatory effect of insecticides on beetle movement was suggested by

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Coaker[8] to explain increases in numbers of trapped carabids.

Understanding the association between insecticides and carabid movement would help to interpret results from studies that focus on or include ground beetles. In addition to their reputation as effective predators, commercial approval of transgenic maize incorporating coleopteran-active toxins in the United States[12] has produced an increased focus on non-target beetles. In the present study, sublethal exposures to pyrethroid insecticides were used to assess the effects of insecticides on movement and population size estimates of carabids. Specifically, experiments were designed to (1) assess changes in aspects of ground beetle movement in the laboratory using an automated video tracking system, and (2) test for related effects on estimates of carabid population size under field conditions.

2 METHODS

Because evidence suggests that both indirect[9,11] and direct[8,10,13] mechanisms could affect population size estimates, steps were taken to reduce the likelihood that carabids were influenced by hunger or prey availability. For laboratory experiments, field-collected beetles were provided artificial diet *ad libitum*. In the first field experiment, beetles were similarly collected and fed prior to being marked and released inside field enclosures. The second field experiment was conducted by trapping only beetles present in the plots (i.e. without mark–release methods), which prevented control of hunger levels among beetles. However, the relatively short duration of both field experiments probably reduced the likelihood of hunger impacting on carabid movement.[9]

2.1 Video tracking trials

Carabid beetles were collected during May and June 2005 using pitfall traps along 25 ha of maize 8 km southwest of Ames, IA, USA. When collections were being made, all beetles were removed within 24 h because of the potential for aggression among beetles in a trap. After collection, carabids were transported to the laboratory and placed into individual specimen cups (65 mm diameter, 237 mL, translucent polypropylene) containing 60 mL of commercial potting soil (Perfect Mix; Spectrum Brands, Inc., St Louis, MO, USA). Beetles were kept in an environmental chamber (23 °C, 14 h photophase, 30% RH) with water (for soil moisture) and food (Diet B; Lundgren *et al.*[14]) added as needed. The large predator *Scarites quadriceps* Chaudior was most common (>75%) and was selected for use in the video tracking trials.

After 3–5 days in the laboratory, beetles were used for video tracking experiments where aspects of beetle movement were monitored for responses to brief exposure to common pyrethroids as they would likely be used near maize planting time (when *S. quadriceps* is most abundant). Laboratory exposures to pyrethroids were considered to be sublethal, as mortality of *S. quadriceps* within 24 h of trials was <5%. Recordings of the paths of individual beetles, called tracks, were made using EthoVision software.[15] Because *S. quadriceps* is nocturnal, transparent plant saucers (356 mm diameter, polyethylene terephthalate) containing *S. quadriceps* were placed on top of a rigid sheet of acrylic glass and lit from below by two infrared light-emitting diode arrays (Tracksys Ltd, Nottingham, UK). White paper between the plastic and the arenas helped diffuse the lighting, and an infrared camera allowed EthoVision to locate the center of gravity for individual beetles as time-series coordinates (x, y) 6 times per second.

For the first experiment, individual beetles were placed into one of three bins (11.4 L, white polypropylene) containing (1) 1.0 L potting soil, (2) 1.0 L potting soil mixed with 26 mg tefluthrin 30 g kg^{-1} granules (Force® 3G; Syngenta Crop Protection, Inc., Greensboro, NC, USA) or (3) 1.0 L potting soil mixed with 51 mg tefluthrin granules. Treatments (2) and (3) correspond respectively to one-quarter and one-half of the concentration of tefluthrin in soil at the maximum label rate to control corn rootworm larvae (*Diabrotica* spp.) at planting (banded application, 0.18 kg AI ha^{-1}). Soil and granule mixtures were used for up to five replicates tested on the same day, although water was added as needed to maintain moisture (up to the original mass of the filled bin), and the contents were mixed manually. After 20 min, beetles were removed and placed into separate saucers used as experimental arenas. Following a brief delay (<5 min), a 60 min track was made for each beetle.

In the second experiment, individual beetles were placed into one of three specimen cups containing dried filter paper (55 mm diameter, 1001-055; Whatman® plc, Brentford, UK) previously dipped into (1) 100 mL water, (2) 100 mL water containing 0.23 mL lambda-cyhalothrin 120 g L^{-1} EC (Warrior®; Syngenta Crop Protection Inc.) or (3) 100 mL water containing 0.45 mL lambda-cyhalothrin EC. Solutions for treatments (2) and (3) correspond respectively to one-quarter and one-half of the concentration of lambda-cyhalothrin at the maximum label rate to control cutworm larvae (Lepidoptera: Noctuidae) at planting (94 L spray ha^{-1}, 0.10 kg AI ha^{-1}). For each replicate, new filter paper circles were dipped into solutions and dried in a chemical hood (face velocity 0.51 m s^{-1}) for 30 min. As in experiment 1, after 20 min of exposure, beetles were removed and placed into the arenas for recording.

The third video tracking experiment investigated the effect of delays between lambda-cyhalothrin exposure and observations, and whether a second exposure would alter carabid movement. Using only the high concentration of lambda-cyhalothrin, repeated shorter (30 min) observations were made 60 min before and 60, 120 and 240 min after an initial (20 min) exposure; a final recording was made 60 min after a second exposure. Between exposure and observation (or between observations), beetles were returned to the specimen cups. At least ten replicates were included for each experiment. Because the potential for mortality at the concentrations and exposure periods used did not appear to be established by previous research, beetles were held for an additional 24 h to assess potential mortality. A summary of the methods for the video tracking trials is shown in Table 1.

2.2 Field trapping experiments

In the first field experiment, plots were established just after maize emergence (21 May 2006) 5 km south of Ames, IA (Johnson farm). Landscaping flags were used to mark eight 9×9 m plots, separated by 36 m. At the center of each plot, a 2×2 m enclosure was created by burying aluminum flashing ($\approx$36 cm height) halfway into the soil. At the same time, pitfall traps were placed at each end of the pieces of flashing, leaving any two adjacent pieces of aluminum flashing connected with a pitfall trap. When a soil-filled cup was placed inside the traps, arthropods could move freely between the enclosure and the area outside; however, without the soil-filled cups, this arrangement collected beetles attempting to leave (or enter) the enclosure. To collect beetles for the first field experiment, pitfall traps were also placed along three nearby (<5 km) maize plots. Adults of the two most common species collected in late May and early June, *S. quadriceps* and *Pterostichus coracinus* Newman, were returned to the laboratory and maintained on artificial diet. Each beetle was also marked with dots of white or orange acrylic paint applied to the elytra with a small paintbrush.

When maize in the field plots (Johnson farm) reached the four-leaf (V4) stage,[16] pitfall traps at the corners of the enclosures were opened (i.e. the soil-filled cups were removed) and a foliar application of lambda-cyhalothrin (0.028 kg AI ha^{-1}) was made to simulate insecticidal control of cutworm larvae in four of the eight plots. After 24 h, the contents of pitfall traps were collected into specimen cups. Subsequently, a cage composed of wood and brass wire cloth[17] containing 2 L of potting soil and 30 marked beetles (15 each of *S. quadriceps* and *P. coracinus* marked with white paint) was placed into the center of each enclosure. The soil in each cage was intended to reduce contact and aggression among the beetles. Further, to reduce the likelihood of agitation dispersal[18] or dispersal to find food, beetles were placed into the cages 1 h prior to release, and artificial diet (40 mL) was positioned just outside the door of each cage, which was opened <10 min after cages were positioned in the enclosures. A second release of 20 marked beetles (ten each of *S. quadriceps* and *P. coracinus* marked with orange paint) per enclosure was made 48 h after the first release. Collections of marked and unmarked beetles were made every 24 h until a total of 6 days had passed since the lambda-cyhalothrin application.

A glyphosate (Roundup®; Monsanto Company, St Louis, MO, USA) application intended for a nearby soybean field was accidentally made to plots at the Johnson farm 7 days after the lambda-cyhalothrin application, precluding additional work at that location. Therefore, the second field trapping trial was conducted 7 km south of Ames, IA (New Dairy farm). The experiment at the New Dairy location employed a different strategy that was judged to be more realistic than the first trial; larger (36×36 m) plots were used without field enclosures or releases of marked beetles. In each plot, five pitfall traps were arranged in an 'X' pattern, with adjacent traps separated by 5–6 m. After an application of permethrin 15 g kg^{-1} granules (Pounce® 1.5G, 0.22 kg AI ha^{-1}; FMC Corporation, Philadelphia, PA, USA) to four of the eight plots, beetles were collected from the traps every 24 h until a total of 6 days had passed since the insecticide application. This experiment was intended to simulate insecticidal control of first-generation European corn borer (*Ostrinia nubilalis* Hübner) larvae with a granular insecticide, which can improve control by collecting in and around the whorl of vegetative stage maize. However, the delay caused by the need to change field locations and an earlier planting date (22 April) at the second location resulted in an application to reproductive stage plants, likely reducing the proportion of permethrin granules reaching carabids near the soil surface.

2.3 Data analysis

For video tracking trials, total distance moved, maximum velocity, meander and percentage of time moving (start velocity >0.50 cm s^{-1}; stop velocity <0.25 cm s^{-1}) were calculated on individual tracks to represent complementary aspects of *S. quadriceps* movement. To remove error produced by system noise and trivial movement, input filters were used with downsampling step = 4 and minimum distance moved = 0.5 cm.[15] No more than one replicate within an experiment was excluded on the basis of inactivity (i.e. percentage of time moving = 0) or mortality within 24 h of trials. Output parameters (total distance moved, maximum velocity, meander and percentage

Table 1. Summary of treatments included in video tracking experiments, 2005

Insecticide	Exposure method	Concentrations[a]	Observation time; delays (min)[b]
Tefluthrin	Granules in soil	Control, low, high	60; <5
Lambda-cyhalothrin	Residue on filter paper	Control, low, high	60; <5
Lambda-cyhalothrin	Residue on filter paper	High	30; 60, 120, 240

[a] See text, Section 2, for details on insecticide mixtures and exposure protocols.
[b] Delays indicate time between end of insecticide exposure and start of video tracking.

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of time moving) from EthoVision were analyzed using SAS software[19] by the MIXED procedure. To meet assumptions regarding normality and equality of variances, transformations for total distance moved ($\log_{10}$) and percentage of time moving (arcsine-square root) were used. For the first and second video tracking experiments, separate analyses of variance tested for effects of insecticide exposure on each dependent variable including replicate as a random effect. Because the third experiment exposed all beetles to insecticides and used individual beetles more than once, a repeated-measures analysis of variance tested for effects of insecticide exposure by using time (within-subject effect). Repeated measurements on individual beetles were related by a heterogeneous compound symmetry covariance structure. For all three experiments, differences among treatments (or times in the third experiment) were assessed using *t*-tests.

Collections of beetles from pitfall traps at both field locations were also analyzed using repeated measures. For the first location (Johnson farm), *S. quadriceps* and *P. coracinus* were pooled for analysis. Separate repeated-measures models tested whether lambda-cyhalothrin treatment (between-subject effect), time (within-subject effect) or a treatment × time interaction were significantly related to the $\log_{10}(x+1)$ number of marked or unmarked beetles captured per plot. At the second field location (New Dairy farm), a similar analysis was used to test for the effects of permethrin application on pitfall trap captures. However, carabid abundance and species composition differed relative to earlier collections; accordingly, all predatory or omnivorous carabids (from Larochelle and Larivière[20]) were pooled over 2 day periods. For both analyses, repeated measures were related by a heterogeneous first-order autoregressive covariance structure, and any significant treatment effects were evaluated with *t*-tests.

3 RESULTS

3.1 Video tracking trials

Brief exposure of *S. quadriceps* to soil-incorporated tefluthrin granules caused significant increases in distance moved, maximum velocity and percentage time moving (Table 2). However, mean separation suggests that only the high concentration (51 mg L^{-1}) significantly differed from the control (Table 3). Lambda-cyhalothrin exposure also increased distance moved, maximum velocity and percentage time moving for *S. quadriceps* (Table 2), and paired comparisons indicate significant differences between the control and both tested concentrations (Table 3).

The third (repeated-measures) experiment with lambda-cyhalothrin exposure showed significant effects of time (i.e. exposure) on distance moved,

Table 2. Results of analyses of variance on beetle movement from video tracking experiments, 2005

Insecticide	Aspect of movement	*F*	df	*P*
Tefluthrin	Distance moved (m)	6.48	2, 18	0.008
	Meander (deg cm^{-1})	0.27		0.768
	Maximum velocity (cm s^{-1})	4.64		0.024
	Time moving (%)	9.51		0.002
Lambda-cyhalothrin	Distance moved (m)	37.40	2, 18	<0.001
	Meander (deg cm^{-1})	1.35		0.280
	Maximum velocity (cm s^{-1})	35.27		<0.001
	Time moving (%)	26.68		<0.001
Lambda-cyhalothrin[a]	Distance moved (m)	20.97	4, 36	<0.001
	Meander (deg cm^{-1})	7.34		<0.001
	Maximum velocity (cm s^{-1})	30.08		<0.001
	Time moving (%)	10.46		<0.001

[a] Second lambda-cyhalothrin experiment includes two exposure periods and repeated-measures on individual beetles.

Table 3. Aspects of *Scarites quadriceps* movement, mean (± SE), from video tracking experiments 1 and 2, 2005[a]

Insecticide	Concentration[b]	Distance moved (m)	Meander (deg cm^{-1})	Maximum velocity (cm s^{-1})	Percentage time moving (%)
Tefluthrin	Control	21.2 (±8.7) B	14.1 (±2.7) A	6.1 (±0.4) B	33.6 (±7.9) B
	Low	30.9 (±13.4) B	14.8 (±2.4) A	6.4 (±0.6) B	40.7 (±6.7) B
	High	75.7 (±19.3) A	12.7 (±1.6) A	8.0 (±0.6) A	70.6 (±8.0) A
Lambda-cyhalothrin	Control	7.9 (±3.2) B	18.2 (±3.1) A	4.4 (±0.5) C	23.8 (±5.0) B
	Low	75.5 (±14.4) A	25.5 (±4.7) A	7.5 (±0.4) B	78.4 (±6.8) A
	High	114.4 (±17.9) A	17.8 (±3.3) A	8.6 (±0.2) A	83.5 (±5.1) A

[a] For each experiment, different letters within a column indicate significant differences (paired *t*-test, $P < 0.05$). Untransformed means are presented for clarity.
[b] See text, Section 2, for details on insecticide mixtures and exposure protocols.

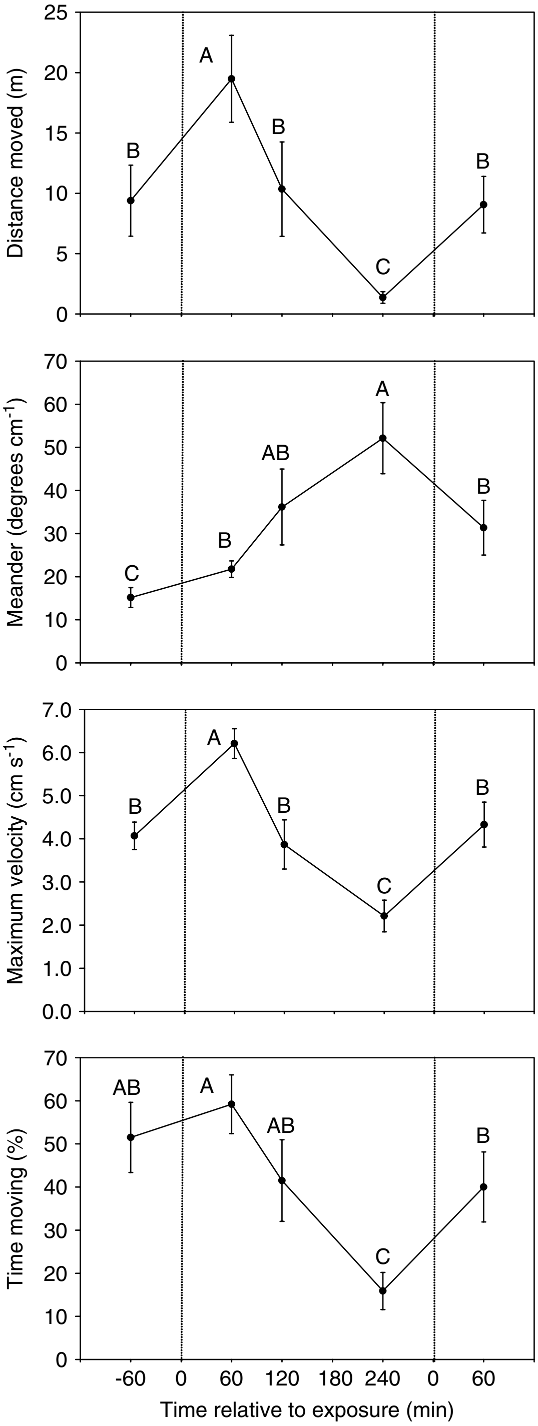

Figure 1. Aspects of *Scarites quadriceps* movement (mean ± SE) from repeated tests of individual beetles, 2005. Dashed vertical lines indicate the timing of insecticide exposures. Different letters within plots indicate significant differences (*t*-test, $P < 0.05$). Untransformed means are presented for clarity.

meander, maximum velocity and percentage time moving (Table 2). In general, means separation suggests that insecticide residues increased movement (distance moved, maximum velocity, percentage time moving) in observations 60 min after insecticide exposure, but caused a decline in activity 240 min after exposure (Fig. 1). The pattern of changes in meander for *S. quadriceps* appeared contrary to the other movement-related parameters (Fig. 1).

3.2 Field trapping experiments

Of the 400 total paint-marked beetles released, 334 (84%) were recovered. The number of *S. quadriceps* and *P. coracinus* recovered was significantly influenced by time (Table 4), with most of the recaptured beetles (294/334 = 88%) collected the day after a release. No significant effect of lambda-cyhalothrin treatment or the treatment × time interaction on the number of marked beetles recaptured was detected. For unmarked *S. quadriceps* and *P. coracinus*, significant effects of time and the treatment × time interaction were detected (Table 4). However, even when treatments were compared within dates (*t*-test), no significant effects of insecticide treatment were apparent. At the second field location, pitfall trapping recovered five carabid species characterized as predatory or omnivorous, including *S. quadriceps*, *Poecilus lucublandus* (Say), *Poecilus chalcites* (Say), *Harpalus pennsylvanicus* (DeGeer) and *Harpalus caliginosus* (Fabricius). Although, 1–2 days after the permethrin application, the number of predatory carabids collected per plot appeared to be greater in the insecticide-treated plots (1.67) compared with the untreated plots (0.97), analysis indicated that the number of beetles collected was not altered by treatment, time or the treatment × time interaction (Table 4).

4 DISCUSSION AND CONCLUSIONS

Video tracking data indicate that brief, sublethal exposures to pyrethroids increase movement of *S. quadriceps*, suggesting the potential for a direct connection between insecticide applications and increases in population estimates based on pitfall-trap captures. While repeated-measures experiments also indicated declines in movement several hours after an initial exposure to lambda-cyhalothrin, a second exposure caused another increase in beetle activity. However, in two field tests with continuous exposure to pyrethroids, no increases in pitfall trap captures of *S. quadriceps* or other predatory carabids were detected.

The increases in *S. quadriceps* activity after exposure to tefluthrin and lambda-cyhalothrin are similar to reports of insecticide-induced repellency and

Table 4. Results of analyses of variance on beetles collected from pitfall traps in field experiments, 2006

Insecticide	Effect	*F*	df	*P*
Lambda-cyhalothrin	Treatment	0.23	1, 6	0.649
(marked beetles)	Time	92.92	4, 24	<0.001
	Treatment × time	0.27	4, 24	0.894
Lambda-cyhalothrin	Treatment	0.36	1, 6	0.572
(unmarked beetles)	Time	20.55	5, 30	<0.001
	Treatment × time	3.94	5, 30	0.007
Permethrin[a]	Treatment	0.17	1, 6	0.691
	Time	1.49	2, 12	0.265
	Treatment × time	2.01	2, 12	0.176

[a] Because of lower abundance, beetles were pooled over 2 day periods.

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hyperactivity of pyrethroids[13,21] and other insecticide classes[22–25] under controlled conditions. In particular, Bayley and Baatrup[22] found changes in movement of an isopod that corresponded to those seen in the first and second video tracking experiments with *S. quadriceps* (increases in distance moved, maximum velocity, percentage time moving), although the period of exposure was much longer (22 h). Hyperactivity resulting from sublethal insecticide exposure usually appears to compromise the ability of predators to feed,[4,23,26] but at least one study suggests a short-term benefit of stimulation for location of hosts by a parasitoid.[25] The third (repeated-measures) video tracking experiment indicated inhibition of *S. quadriceps* movement and an increase in meander 240 min after lambda-cyhalothrin exposure. This decrease in directed movement seems to be similar to observations of temporary ataxia in spiders by Shaw *et al*.,[4] but the second insecticide exposure precluded estimating the duration of this effect.

Several factors could help explain why lambda-cyhalothrin or permethrin applications did not significantly increase carabid collections from pitfall traps in the field. For the marked beetles recaptured in pitfall traps, the high recovery (84% of *S. quadriceps* and *P. coracinus* released, most within 24 h of release) in the untreated plots suggests any increase would likely be too small to detect. Whether the high proportion of recaptures was caused by agitation of the beetles or some other factor, any future tests would require modifications to retain a greater proportion of the beetles (although a similar test by Heneghan[10] suggests that the general design was appropriate). For unmarked beetles collected in the Johnson farm experiment, it is possible that the area of the treated plots was too small, allowing movement of beetles from outside the treated areas to interfere.[27] The permethrin application to larger (36×36 m) plots at the New Dairy farm would likely fail to detect any existing treatment effects owing to a tenfold decrease in the number of predatory carabids collected. Although collections of ground-dwelling predators (mostly carabids) in the study area declined from June to July,[28] the number of ground beetles collected at the second field location was lower than anticipated.

However, the simplest explanation for the disagreement between laboratory and field results is that reported increases in population size estimates of natural enemies after insecticide applications are more likely attributable to indirect mechanisms, including scavenging,[11] reduced competition, hunger,[9,29] or impairment of hosts.[5] Another possible mechanism is hormesis, a dose–response phenomenon in which very low levels of substances considered harmful may elicit positive biological responses. Hormesis differs from repellency, having a modest positive impact (30–60%) at exposure levels well below those that cause adverse effects.[30] Considering both the diversity of possible causes and the reported frequency with which insecticides increase population estimates of carabids, unexpected population-level effects in other natural enemy groups should be interpreted carefully. Perhaps the simplest solution is to collect additional data that evaluate populations using methods less influenced by arthropod activity (soil and surface litter samples; Dively[5]) or explore the mechanism of apparent changes (gut-contents analysis; Chiverton[9]).

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REFERENCES
1 Van Driesche RG and Bellows TS, Natural enemy conservation, in *Biological Control*. Chapman and Hall, New York, NY, USA, pp. 105–127 (1996).
2 Waage J, The population ecology of pest–pesticide–natural enemy interactions, in *Pesticides and Non-target Invertebrates*, ed. by Jepson PC. Intercept Limited, Andover, UK, pp. 81–93 (1989).
3 Elzen GW, Sublethal effects of pesticides on beneficial parasitoids, in *Pesticides and Non-target Invertebrates*, ed. by Jepson PC. Intercept Limited, Andover, UK, pp. 129–150 (1989).
4 Shaw EM, Waddicor M and Langan AM, Impact of cypermethrin on feeding behaviour and mortality of the spider *Pardosa amentata* in arenas with artificial 'vegetation'. *Pest Manag Sci* **62**:64–68 (2006).
5 Dively GP, Impact of transgenic VIP3A × Cry1Ab lepidopteran-resistant field corn on the nontarget arthropod community. *Environ Entomol* **34**:1267–1291 (2005).
6 Lopez MD, Prasifka JR, Bruck DJ and Lewis LC, Utility of ground beetle species as indicators of potential non-target effects of Bt crops. *Environ Entomol* **34**:1317–1324 (2005).
7 Holland JM and Smith S, Sampling epigeal arthropods: an evaluation of fenced pitfall traps using mark–release–recapture and comparisons to unfenced pitfall traps in arable crops. *Entomol Exp Appl* **91**:347–357 (1999).
8 Coaker TH, The effect of soil insecticides on the predators and parasites of the cabbage root fly (*Erioischia brassicae* (Bouché)) and on the subsequent damage caused by the pest. *Ann Appl Biol* **57**:397–407 (1966).
9 Chiverton PA, Pitfall-trap catches of the carabid beetle *Pterostichus melanarius*, in relation to gut contents and prey densities, in insecticide treated and untreated spring barley. *Entomol Exp Appl* **36**:23–30 (1984).
10 Heneghan PA, Assessing the effects of an insecticide on the activity of predatory ground beetles, in *Interpretation of Pesticide Effects on Beneficial Arthropods*. Association of Applied Biologists, Wellesbourne, UK, pp. 113–119 (1992).
11 Bel'skaya EA, Zinov'ev EV and Kozyrev MA, Carabids in a spring wheat agrocenosis to the south of Sverdlovsk oblast and the effect of insecticide treatment on their populations. *Russ J Ecol* **33**:38–44 (2002).
12 *Bacillus thuringiensis Cry3Bb1 Protein and the Genetic Material Necessary for its Production (Vector ZMIR13L) in Event MON863 Corn (006484)*. [Online]. US Environmental Protection Agency (USEPA) Fact Sheet (2003). Available: http://www.epa.gov/pesticides/biopesticides/ingredients/

factsheets/factsheet_006484.htm [accessed 27 February 2007].

13 Wiles JA and Jepson PC, Sublethal effects of deltamethrin residues on the within-crop behavior and distribution of *Coccinella septempunctata*. *Entomol Exp Appl* **72**:33–45 (1994).

14 Lundgren JG, Duan JJ, Paradise MS and Wiedenmann RN, Rearing protocol and life history traits for *Poecilus chalcites* (Coleoptera: Carabidae) in the laboratory. *J Entomol Sci* **40**:126–135 (2005).

15 *EthoVision Video-tracking System for Automation of Behavioral Experiments: Reference Manual Version 3.0*. Noldus Information Technology bv., Wageningen, The Netherlands (2002).

16 Ritchie SW, Hanway JJ and Benson GO, How a corn plant develops. Iowa State University of Science and Technology Special Report No. 48, 21 pp. (1997).

17 Prasifka JR, Sumerford DV, Hellmich RL, Lewis LC and Calvin DD, Sampling European corn borer (Lepidoptera: Crambidae) larvae from seed corn drying bins for Bt resistance monitoring. *Southwest Entomol* **31**:269–279 (2006).

18 Turchin P, *Quantitative Analysis of Movement*. Sinauer Associates, Sunderland, MA, USA (1998).

19 *SAS OnlineDoc, Version 8*. SAS Institute, Inc., Cary, NC, USA (1999).

20 Larochelle A and Larivière MC, *A Natural History of the Ground Beetles (Coleoptera: Carabidae) of America North of Mexico*. Pensoft Publishers, Sofia, Bulgaria (2003).

21 Longley M and Jepson PC, The influence of insecticide residues on primary parasitoid and hyperparasitoid foraging behaviour in the laboratory. *Entomol Exp Appl* **81**:259–269 (1996).

22 Bayley M and Baatrup E, Pesticide uptake and locomotor behaviour in the woodlouse: an experimental study employing video tracking and ^{14}C-labelling. *Ecotoxicology* **5**:35–45 (1996).

23 Umoru PA, Powell W and Clark SJ, Effect of pirimicarb on the foraging behaviour of *Diaeretiella rapae* (Hymenoptera: Braconidae) on host-free and infested oilseed rape plants. *Bull Entomol Res* **86**:193–201 (1996).

24 Singh SR, Walters KFA and Port GR, Behaviour of the adult seven spot ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae), in response to dimethoate residue on bean plants in the laboratory. *Bull Entomol Res* **91**:221–226 (2001).

25 Rafalimanana H, Kaiser L and Delpuech J, Stimulating effects of the insecticide chlorpyrifos on host searching and infestation efficacy of a parasitoid wasp. *Pest Manag Sci* **58**:321–328 (2002).

26 Dempster JP, The sublethal effect of DDT on the rate of feeding by the ground-beetle *Harpalus rufipes*. *Entomol Exp Appl* **11**:51–54 (1968).

27 Prasifka JR, Hellmich RL, Dively GP and Lewis LC, Assessing the effects of pest management on non-target arthropods: the influence of plot size and isolation. *Environ Entomol* **34**:1181–1192 (2005).

28 Prasifka JR, Schmidt NP, Kohler KA, Hellmich RL, O'Neal ME and Singer JW, Effects of living mulches on predator abundance and predation on sentinel prey in a corn–soybean–forage rotation. *Environ Entomol* **35**:1423–1431 (2006).

29 Grum L, Spatial differentiation of the *Carabus* L. (Carabidae, Col.) mobility. *Ekol Pol* **19**:1–34 (1971).

30 Calabrese EJ and Baldwin LA, Hormesis: the dose–response revolution. *Annu Rev Pharmacol Toxicol* **43**:175–197 (2003).